

SEXUAL DIFFERENCES IN HABITAT PREFERENCE  
AND BEHAVIOR OF *OENEIS CHRYXUS*  
(NYMPHALIDAE: SATYRINAE)

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**ABSTRACT.** Individual *Oeneis chryxus* were captured, marked, released, and observed during 1988 and 1990 at a site in the Rocky Mountains of central Colorado at 2700 m. Habitat preferences were analyzed in the context of hilltopping and territoriality. Males showed a clear preference for rocky ridge tops, whereas most females were found in grassy meadows. Male and female flight patterns differed significantly. Males and females responded differently to conspecifics and to other species. Males defended territories, females did not.

**Additional key words:** hilltopping, territoriality, flight pattern, mate-searching, arctic butterfly.

*Oeneis chryxus* (Doubleday and Hewitson) is a small, orange-brown, cryptically-colored butterfly. It prefers open, sunny habitats, and is arguably the most variable of the "arctics" in terms of color, markings, habitat, range, and behavior. This species is found in northern or montane environments characterized by short summers and requires two years to mature. At least one population in Colorado is synchronized on a biennial cycle, with adults absent in odd numbered years (Emmel et al. 1992, Clayton & Petr, unpublished). Scott (1986) reported that population size is greater during even-numbered years in Colorado and in odd-numbered years in northwest Wyoming and California; alternating population size is not apparent in Michigan and Manitoba (Scott 1986).

Masters and Sorensen (1969) characterize *O. chryxus* as a prairie and steppe species with a tendency to move into other habitats such as forests and mountaintops. At Stagecoach Meadows, on the west slope of the Colorado Rockies (Gunnison County, Colorado), *O. c. chryxus* occurs in open meadows but is found more often in the "tension zone" between meadow and forest, characterized by fallen trees and open areas for perching (Masters & Sorensen 1969). Scott (1986) reported *O. c. chryxus* perching on hilltops or ridge tops, but also observed the species perching in gulches near timberline in the San Juan Mts., Colorado (perhaps to avoid harsh winds that sweep the crests). Other species of *Oeneis* (e.g., *O. melissa* (Fabricius)) also are known for their hilltopping habits (Troubridge et al. 1982). Dunlap (1962) and Knapton (1985) studied *O. c. strigulosa* McDunnough in Algonquin Park, Ontario, Canada, where it reportedly does not exhibit hilltopping behavior but defends perch sites in open sandy or stony spots in relatively flat terrain. In addition, territorial behavior has been reported for *O. chryxus* by Dunlap (1962), Troubridge et al. (1982), Knapton (1985), and Mas-

ters and Sorensen (1969), and for several other species of *Oeneis* by Guppy (1962), Masters and Sorensen (1969), and Troubridge et al. (1982).

Based on studies of *O. c. chryxus* in a montane community near Florissant, Colorado, we report on sexual differences in habitat preference, territoriality, and behavior.

## MATERIALS AND METHODS

Our study area was located 12 km S of Florissant, Colorado, at an elevation of 2670–2707 m. It was traversed by a path 1065 m long, connecting three ridge tops (A, B, & C) and two meadows (MB & MC). The study area covered 102,850 m<sup>2</sup> of which ridges were 10,450 m<sup>2</sup> and meadows were 18,400 m<sup>2</sup>.

The ridges were characterized by rock outcroppings, pines (*Pinus ponderosa* Laws.; Pinaceae), aspens (*Populus tremuloides* Michx.; Salicaceae), and open patches of stony soil sparsely vegetated with low grasses and forbs. Meadows were located at the base of large gulches where soil was deeper, richer, and wetter. Meadows supported grasses and forbs with shrubby cinquefoil (*Potentilla fruticosa* L.; Rosaceae) and other shrubs sparsely distributed throughout, and small aspens and pines around the edges.

Observations were made on 4 days (5–8 July) in 1988 and on 13 days (24 June–6 July) in 1990. A total of 196 individuals were captured, marked, and released. Individual *O. c. chryxus* were numbered on the underside of the hindwing using red or black Sharpie permanent marker pens (Sanford) or a "Silver-Marker" paint-pen (Pilot) and identified later with binoculars. Each individual's number, sex, location of capture, and the time, date, and location of all sightings and behaviors were recorded. Some individuals were sighted 10 or more times per day but were counted only once per day unless they moved to a different ridge or meadow. This procedure prevented biases from extended observations at more active sites.

## RESULTS

### Habitat Preference

**Ridge tops and meadows.** Males were found more frequently on ridge tops, and females were found more frequently in meadows (Fig. 1; Chi Square with Yates correction = 157.5,  $P < 0.001$ ). The pattern of sex distribution on the ridges was the same in 1988 and 1990.

Females were more sedentary than males. Fifteen percent (26 of 173) of adults captured in 1990 were females, but only 10.5% of the sightings (29 of 275) were females.

**Elevation and exposure.** Fig. 2 gives the number of male sightings

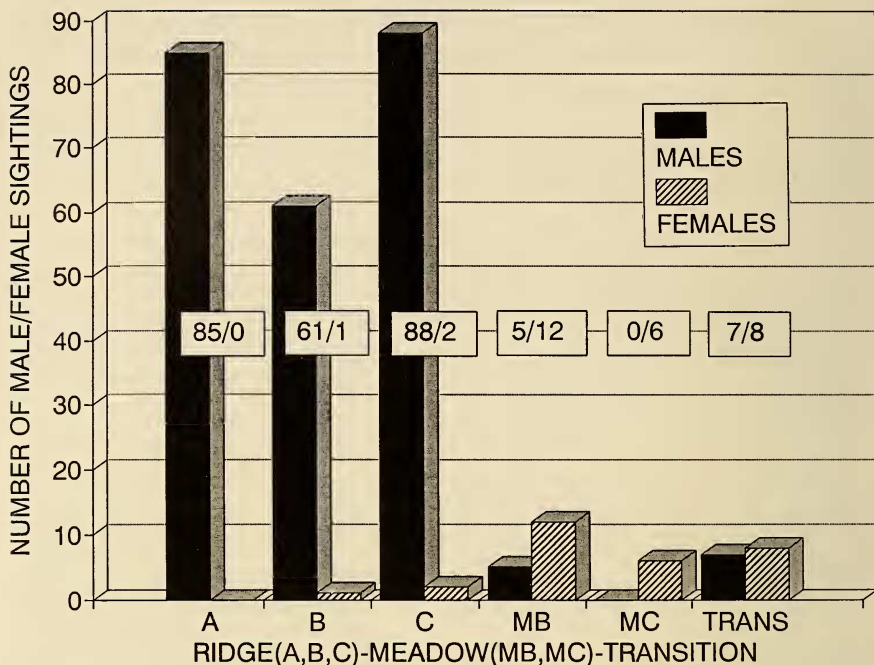
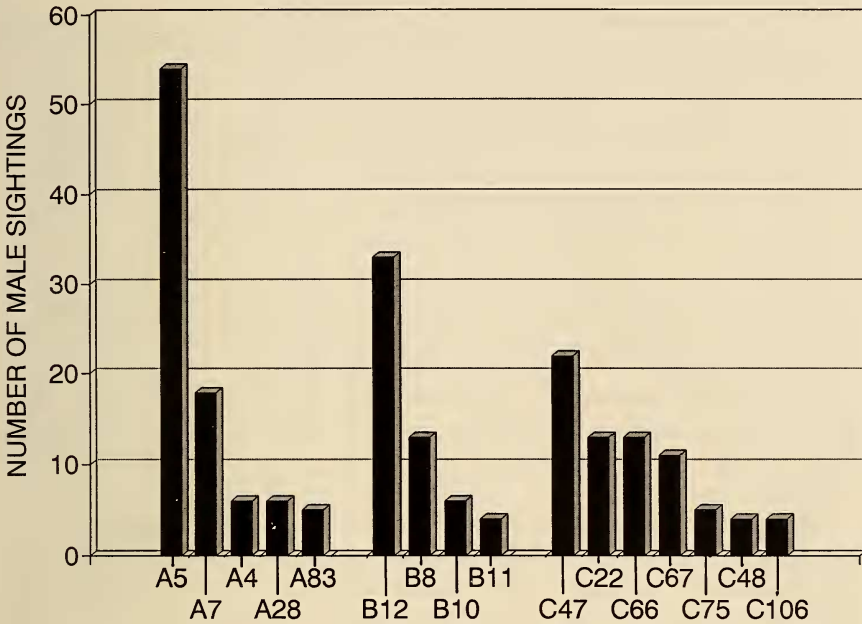


FIG. 1. Habitat distribution of male and female *Oeneis chryxus chryxus* sightings at three ridge tops, two meadows and intermediate areas (TRANS). Numbers in boxes indicate the proportion of males to females for the 1990 season. Individuals were scored only once per day.

at the more active perch sites during the 1990 season. Elevation of perch sites and number of male sightings showed a significant positive correlation (Spearman Rank Correlation,  $P < 0.05$ ). Perch sites A5, B12, and C47 were the three most frequently occupied and also were the highest sites on the three ridges of the study area. Ridge C was not studied in 1988, but activity on Ridges A and B showed the same pattern in 1988 as in 1990, with sites A5 and B12 being the two most active sites, and A7 and B8 being next most active. All active sites (Fig. 2) were open and relatively free of ground cover and overhead vegetation.

#### Behavioral Differences

**Flight patterns.** Females seem to have a slower wing-beat, fly with less undulation, and have straighter flight paths than males. By contrast, males circled and returned quickly to their perches after engaging other butterflies or if disturbed by us. These simple differences were used to correctly predict sex of 60/60 male and 11/12 female *O. c. chryxus* before capture ( $P < 0.001$ , Chi Square = 45.9). When stalked or disturbed, males sometimes abandoned the perch and disappeared into



THE MOST ACTIVE RIDGE SITES

FIG. 2. Number of *Oeneis chryxus chryxus* male sightings at the most frequented sites on three ridges. Sites A5, B12, and C47 were the highest points on Ridges A, B, and C. Only sites with four or more sightings are shown. Individuals were scored only once per day.

vegetation; female wing beat frequency increased or became more erratic as they attempted escape. Prediction of sex was not attempted if an individual gave conflicting signals. Predictions were recorded only during the last nine days of the 1990 field observations.

**Chases and spirals.** Any butterfly moving near a male *O. c. chryxus* elicited a chase. Usually the intruder took a direct path away from the perch site with the resident in pursuit. The chase often turned into a spiraling flight with two, or occasionally three, individuals twirling in tight circles around each other. Some spirals lasted more than 45 seconds and did not end until the butterflies were well above the treetops, as high as 30 m above ground. Spirals ended with one or both participants diving sharply toward the ground. The resident returned to the perch site more often than the intruder (Table 1, Chi Square = 98.7,  $P < 0.001$ ). A resident was defined as a marked *O. c. chryxus* male with a recent history of occupancy and successful defense of the perch site against conspecifics.

Nine females captured in meadows were released on ridges and

TABLE 1. A comparison of site tenacity for resident *Oeneis chryxus chryxus* and intruding conspecifics. A resident was defined as a marked *O. c. chryxus* male with a recent history of occupancy and successful defense of the perch site.

Flight season	Return to perch site			Number of encounters
	Resident only	Intruder only	Resident and intruder	
1988	40 (88.8%)	1 (2.2%)	4 (8.8%)	45
1990	114 (77.0%)	3 (2.0%)	31 (20.9%)	148

observed. Most females fled resident males and were pursued in long chases or spiral flights. Three of the nine pursued females landed on the trunks of trees or in branches as high as 10–12 m, and the resident males returned to their perches. Only one male from more than 300 male/male encounters landed in a tree. Two of the released females landed on the ground where the pursuing males approached and attempted to mate.

Females were never observed to initiate chases or defend territories. One female was observed for an hour while nectaring on shrubby cinquefoil in a meadow. A grasshopper and six butterflies (a skipper, two angle-wings, a sulfur, a little blue, and a copper) flew within 10–30 cm of her but elicited no response. All males we observed gave chase when approached by butterflies, moths, birds, falling leaves, and even pebbles tossed near the perch.

#### DISCUSSION

Marked butterflies could be identified with binoculars, making it unnecessary to recapture them or to disrupt their activities. Morton (1984) found that adding marks of different color or size to the cryptic underwings of five butterfly species did not change the statistical probability of sighting them on subsequent days. Recapture involving handling, however, did reduce the frequency of sightings in his study.

Dunlap (1962) and Knapton (1985) studied *O. c. strigulosa* in Algonquin Park, Ontario, Canada, where it reportedly does not show hilltopping behavior. Both Dunlap's and Knapton's observations were made along an abandoned railroad right-of-way, raised slightly above the surrounding area and providing perch sites free of vegetation. Baughman and Murphy (1988) show that hills need not be high to orient a butterfly's movements and to evoke hilltopping. It could be argued that the Ontario population of *O. c. strigulosa* was hilltopping on the raised roadbed, but it would be difficult to make that argument for the Stage coach Meadow population of *O. c. chryxus* on the west slope of the Colorado Rockies, because they defend perches considerably below available peaks (Masters & Sorensen 1969). Whether the behavioral



variability between populations reflects genetic differences or is in response to differences in habitat, elevation, or topography is unknown.

*Oeneis c. chryxus* hilltop near Florissant, Colorado, although features other than elevation, such as bare ground and lack of surrounding trees or bushes, add to the attractiveness of perch sites. On ridge A, site A7 was at the same elevation as A5 and only 50 m away, but had significantly fewer male sightings (Fig. 2; Chi Square = 18.0,  $P < 0.001$ ). The more active site (A5) had slightly less cover on the periphery and was at the head of a valley leading from a meadow. Site B8, on ridge B, was slightly lower but had more activity than adjacent sites B10 and B11. B8 was free of vegetation and atop a large rock (2 m high and 5 m in diameter), with bare ground sloping downhill for 20–25 m. B10 and B11 were bounded by bushes and trees. The distribution of *O. c. chryxus* males at sites on Ridge C are strongly correlated with elevation. Site C47 was at the peak; sites C22, C66, and C67 were at nearly equal elevations but lower than C47, and the remaining sites were even lower on the ridge.

A female would encounter a male about 15–30 times as frequently on ridges as she would in meadows. This estimate is based on male sightings and is corrected for observation times in the two habitats. Weather conditions permitted an average flight period slightly longer than five hours per day; thus, in 10 to 20 minutes a female would encounter as many males on ridges as she would in five hours (an entire day's flight period) in meadows. Hilltopping for mate location greatly reduces a female's energy expenditure and exposure to predation.

Hilltopping is well-documented for butterfly species and other insects as an efficient strategy for bringing mates together (Alcock 1987, Shields 1967, Lederhouse 1982, Scott 1968, Thornhill & Alcock 1983, Wickman 1987, 1988). We assume that virgin female *O. c. chryxus* hilltop for mating, but quickly return to meadows for oviposition on the abundant grasses that are their larval food plants. Wickman (1988) showed that virgin female *Lasiommata megera* (L.) (Satyrinae) fly uphill to where males perch, but cease to do so after mating.

Wickman (1986, 1987, 1988) and Wickman and Wiklund (1983) demonstrated that females of three genera of satyrines in Europe mate soon after eclosing and usually only once. Wiklund (1982) also showed that following mating, female *Aphantopus hyperanthus* (L.) (Satyrinae) become more cryptic, evasive, and resistive to male contact. Similar behaviors in *O. c. chryxus* likely account for the smaller number of females found in our study and in collections we have examined.

Male *Coenonympha pamphilus* (L.) (Satyrinae) defending territories achieve more matings than do males without territories (Wickman 1985). Ehrlich and Wheye (1986, 1988) present an interesting exception

in which hilltopping and territoriality result in lower mating success for *Euphydryas editha* (Boisduval) (Nymphalinae) during years of high population density (also see Scott 1968).

Territoriality in insects, and specifically in butterflies, has been questioned on the basis of the primitive phylogenetic position of the group and a lack of defensive accouterments (Scott 1974, 1986, Suzuki 1976). However, an individual's ability to maintain a territory can be decided simply by the response of conspecifics. The chases and spirals initiated by resident males are effective because intruders tend to leave directly and quickly (Table 1). The most active sites were at times contested for by two, rarely three, sparring males; but the resident initiated most of the chases, occupied the preferred perch, and enjoyed the most occupancy time. Such contests always were resolved, usually with one encounter. Encounters from which both resident and intruder returned to the perch site involved a short series of engagements from which the resident (usually) returned alone the final time. Extended observations at the more active sites in 1990 account for the increased proportion of encounters where both resident and intruder returned (Table 1).

It is unlikely that *O. c. chryxus* males can distinguish gender or even species from the perch, demonstrated by the fact that they chase skippers, swallowtails, birds, falling leaves, or tossed pebbles. Scott (1986) calls chases and spirals "potential courtship forays." The simplest explanation for these forays probably involves a fixed-action pattern (pursuit), coupled to a sign stimulus (movement) via an innate releasing mechanism (Colgan 1989). Once initiated, the behavioral sequence exhibited by the resident is switched to "sparring" by intruder males, "courtship" by females, and "break off" by other species and inanimate objects. The quickness with which resident males attempted to mate females landing on the ground suggests that males discriminate the sex of conspecifics in flight. Occasionally, sparring males landed near one another but two males were never observed to make physical contact on the ground.

The perching male does discriminate some features of intruders. He seldom chases dipterans or hymenopterans even though some are as large as some butterfly species that are chased. The most obvious difference is wing beat frequency. *Oeneis c. chryxus*, other butterflies, moths, and skippers have fluttering, undulating flight patterns and are chased. Bees and flies at most elicited brief, quickly aborted chases, as did pebbles tossed above perching males.

It is axiomatic that benefit must exceed the cost of a behavior (Carpenter 1976). The resource(s) contested for at these perch sites has not been identified unquestionably, but the most likely resource is "mates."

Ridges provide no apparent advantage for food, shelter, thermoregulation, oviposition sites, or freedom from predators.

The habitat and behavioral differences we have described for *O. c. chryxus* indicate a reduced time and energy expenditure for females. Males are found at predictable, easily-located sites (ridges); females are found away from males in more protected sites (meadows) where they are less likely to be disturbed while ovipositing. Males spend much energy and risk greater exposure defending perch sites against competing conspecific males, which suggests that natural selection pays males well for territorial defense (Riechert 1988).

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